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Genetic resistance and tumour morphology in birch infected with *Taphrina betulina*

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Abstract

Witches' broom of birch (*Betula* spp.) caused by *Taphrina betulina* is an understudied disease that causes the formation of woody tumours, from which ectopic axillary buds and branches grow to form a broom-like structure. We have addressed two aspects of this disease using naturally infected mature trees in the field. Broom symptoms offer a convenient means of scoring susceptibility in the field. Variation in broom symptom presentation suggests possible variation in resistance against witches' broom disease. We tracked the local distribution of susceptible individuals among 721 trees at 159 independent sites. The analysis supports the hypothesis that there was genetic resistance segregating in these birch populations. Anatomical changes in broom symptom bearing branches of European silver birch (*Betula pendula*) were also addressed by comparing sections of tissues from three locations in the same branch, which were normal, swollen in infected tissue adjacent to a tumour, and inside a tumour. Examination of tumours revealed disorganized and swollen xylem, expanded secondary phloem and expanded periderm. Swollen tissues newly infected from spreading disease adjacent to tumours exhibited enhanced growth only in secondary phloem and the periderm, which also exhibited distortions. This finding suggests that tumour formation and possibly pathogen colonization may initiate in these tissues.

KEYWORDS
Betula pendula, birch, disease symptoms, genetic resistance, *Taphrina betulina*, tumour growth, tumours, witches' broom disease

1 | INTRODUCTION

Witches' broom disease, caused by *Taphrina betulina* Rostrup, forms characteristic broom symptoms on the branches of birch (*Betula* species; Figure 1a; Fonseca & Rodrigues, 2011; Mix, 1949). *Taphrina betulina* has been shown to produce the plant growth regulators cytokinin and auxin (Kern & Naef-Roth, 1975), which are widely thought to be involved in broom formation, although this has not been formally demonstrated. *Taphrina* species have a dual lifestyle, invading their hosts in the infectious dikaryotic hyphal form, but living as neutral phyllosphere residents in their haploid yeast form for most of the growing season (Fonseca & Rodrigues, 2011; Mix, 1949). Typically, *Taphrina* hyphae are annual, and after completing the sexual cycle, the yeast forms overwinters on host plant surfaces (Fonseca & Rodrigues, 2011). However, *Taphrina* species that cause witches' brooms, including *T. betulina*, also cause perennial infections by invading and overwintering in woody tissues (Fonseca & Rodrigues, 2011). Birch, especially European silver birch (*Betula pendula* Roth), although native to Europe, is widely distributed in northern Eurasia, where it is important both

FIGURE 1 Appearance of witches' broom disease on *Betula* species. (a) Growth habit of *Betula pendula* showing typical witches' broom symptoms. (b) Close up of an exceptionally large (approximately 1 m in diameter) broom. (c) Detail of a typical witches' broom. (d) All ectopic branches of the broom in panel c were removed revealing the central tumour. (e) The tumour in panel d was cut open revealing the internal woody structure. Note, the extensive vascular tissue feeding the many ectopic buds and branches

TABLE 1 Host range of European *Betula* species infected by *Taphrina betulina* resulting in witches' broom

B. pendula	*B. pubescens*	*B. intermedia* Hartm. (*B. nana x B. pubescens*)
Dingley, 1970	Mix AJ., 1949	Selbman et al., 2014
Gjaerum et al., 1964	Jump & Woodward., 1994	Rodrigues & Fonseca., 2003
Bacigálová et al., 2005	Sałata., 1974	Mix AJ., 1949
Wroblewski., 1925	Jeschková.,1957	
Starmachowa., 1963	Spanos & Woodward., 1994	
Mix AJ., 1949		
Zerova., 1969		

environmentally and as a timber commodity (Hynynen et al., 2009; Zohren et al., 2016). Birch has also been developed as a genetic model tree that can be used for forward genetic studies (Alonso-Serra et al., 2020) and genomics (Salojarvi et al., 2017; Wang et al., 2013), making it an attractive system for studies of pathogen interactions with forest plant species. *T. betulina* is known to infect multiple birch species, including silver birch, downy birch and some hybrids (Table 1). A few studies have addressed the effects of this disease. Infection of downy birch (*B. pubescens* Ehrh.) with *T. betulina* was associated with significant reduction in wood development, vigour and quality (Spanos & Woodward, 1994), which may reduce production under birch short rotation forestry programmes (McKay, 2011). However, this disease is understudied and many basic processes of *T. betulina* biology and its pathogenesis on birch remain undefined. Large variation in symptom development, apparent as the number and size of brooms presenting on an individual tree, can be observed in nature, providing anecdotal evidence for genetically encoded resistance segregating in birch populations. However, it remains unclear if this phenomenon is due to genetic resistance in the host, or other factors. Jump and Woodward (1994) examined some aspects of infected woody tissue anatomy and histology in downy birch, but symptom formation has not been addressed in other birch species. Here, we focus on the structure of *T. betulina* -infected woody tissues of

B. pendula and the possibility of genetic resistance segregating in populations of birch in the field.

2 | MATERIAL AND METHODS

2.1 | Field studies

We have assembled a collection of birch trees showing witches' broom symptoms. As indicated (Table S1), this collection comprises both wild individuals in natural populations and planted ornamental individuals distributed throughout the greater Helsinki metropolitan area (Figure 2a), including the island of Isosaari, which lies off the southern coast of Helsinki (Figure 2b). This survey was not comprehensive and the sites have accumulated from years of noting the locations of infected trees. Many of these individuals are heavily infected (>5 large brooms). These 180 distinct sites were defined by one infected individual in the centre, around which all birch trees within a 10 m radius were counted and scored as symptomatic when witches' brooms were present or asymptomatic when free of broom symptoms. Twenty-one sites in the collection were excluded from analysis as no other birch trees occurred within a 10 m radius of an infected individual. Birch species examined in this field study were primarily European silver birch (*B. pendula)* but downy birch (*B. pubescens*) were also included. Only mature trees greater than 10 m in height were counted. To facilitate simple and accurate scoring of broom symptoms in the upper branches, most trees were evaluated and counted during months when leaves were not present. These data were used to test for the presence of genetic resistance to *T. betulina* in birch populations. We reasoned that trees growing in the vicinity of an infected individual would have been exposed to similar *T. betulina* genotypes, inoculum load and environmental conditions. These factors being equal, any observed variation in susceptibility is then most likely explained by host genotype. These data allowed us to test the predictions of two competing models. In the first, if susceptibility is determined by pathogen genotype, inoculum load and environmental conditions, infected individuals would be clustered at sites where conditions were favourable for infection. In the second, susceptibility is determined by the host genotype resulting in mixtures of symptomatic and asymptomatic individuals at most sites. Models for genetic resistance and environmental effects were differentiated using a chi-squared test of goodness of fit with RStudio (https://rstudio.com/).

2.2 | Tumour morphology

Samples of tumour-bearing branches were collected from three different *B. pendula* individuals (Table 2). Tumour morphology was examined by sectioning each sample at three different positions across a developmental gradient for the tumour; specifically, (I) the phenotypically normal part of the stem, (II) in the swollen tissue near the tumour and (III) within the tumour (Figure 3). The three sampled *B. pendula* individuals (Table 2) were confirmed as *B. pendula*

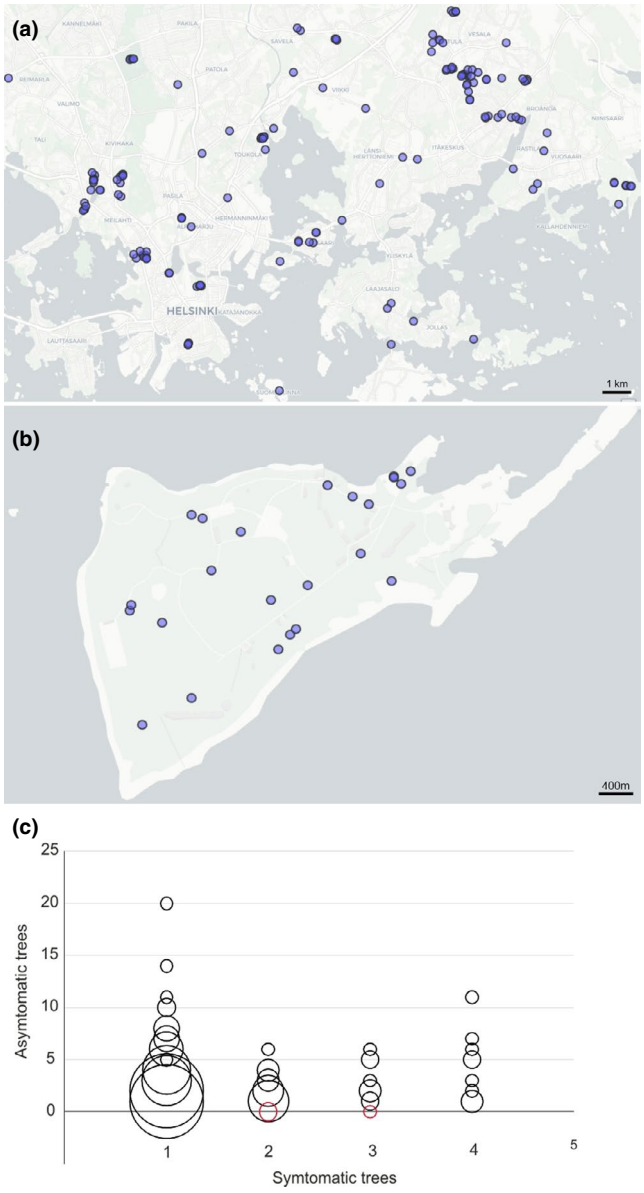

FIGURE 2 Distribution of individuals exhibiting witches' broom symptoms in local populations of birch. (a) Map of the sites in Helsinki each defined by a single witches' broom disease infected birch individual, around which all birch within a 10 m radius were scored for the presence/absence of witches' broom disease. See Table S1. (b). Several sites were also scored on the island of Isosaari, south of Helsinki. (c) Bubble plot summarizing the local distribution of symptomatic and asymptomatic trees in populations within each site. The size of each bubble is proportional to the number of sites with the indicated number of trees in each class. Sites with only symptomatic trees are highlighted in red. Analysis of the data in (c) with Pearson's chi-squared goodness of fit test with Yates' continuity correction rejected the null hypothesis that pathogen exposure and environmental conditions determine the distribution of susceptibility (A, sites with only susceptible trees—B, sites with segregation of resistance, i.e. mixed susceptible and resistant: Observed A 3, B 156, expected A 159, B 0; $\chi^2 = 302.31$, df = 1, p-value <$2.2e^{-16}$)

TABLE 2 Samples of *B. pendula* with witches' broom disease used for examination of tumour morphology[a]

Sample number	Location[b]	Age[c]	GPS Coordinate	Area[d]	Date[e]
1	Merirastilantie	5 years	60° 12' 4.197"N 25° 7' 41.720"E	Natural	05.2019
2	Harbonkuja	5 years	60° 11' 58.357"N 25° 7' 32.544"E	Natural	05.2019
3	Isosaari	8 years	60°05'50.0"N 25°02'42.4"E	Natural	07.2020

[a]Samples were used for analysis presented in Figures 3–5.

[b]Locations of tree sampling sites according to the name of the street or district in the greater Helsinki region.

[c]Approximate age of the sampled branch in years.

[d]Sites were categorized either as; natural—when the site represented naturally occurring populations in green areas, or as planted—when the trees were ornamental and obviously resulted from human activity.

[e]The month and year that the trees were sampled.

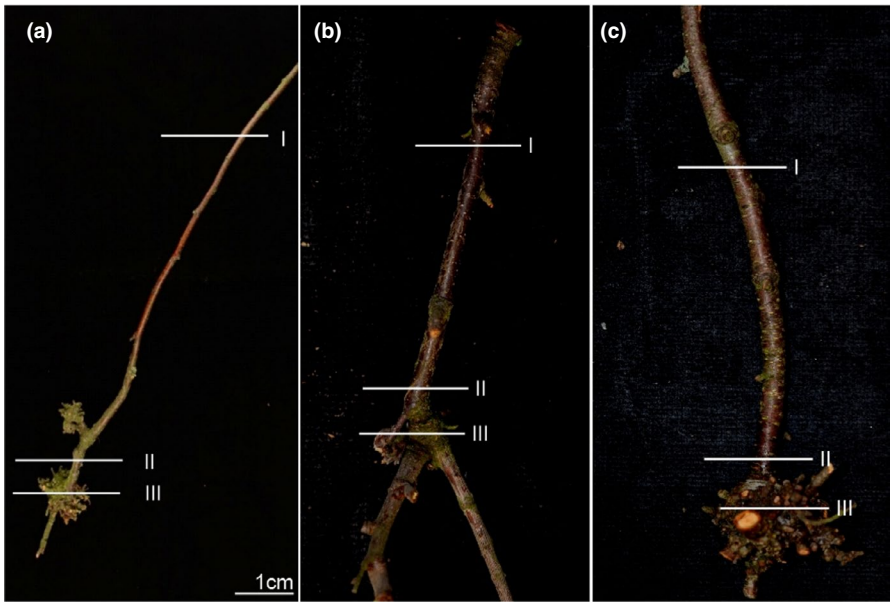

FIGURE 3 Infected *B. pendula* branch samples used in structural studies. This figure depicts the three witches' broom bearing branches listed in Table 2; (a) sample one, (b) sample two and (c) sample three. All side branches within the broom were removed to expose the central tumour. The top of the photograph is proximal to the tree stem. The three positions (I-III) used in sectioning are indicated; (I) healthy tissue; (II) tissue adjacent to the tumour (note, tissue is swollen and diseased in panels a and b, but not c); (III) through the tumour. Scale bar (1 cm; valid for all panels)

using multiple traits over the growing season; that is, overall trunk and branching growth habitus in early spring, twig bark morphology on new growth in spring and seed morphology in late summer. Stems with symptoms were collected, stored on ice during transport and stored at −70°C until processing. Wood samples were selected and cut with a precision hand saw into blocks for sectioning to a thickness of 20 µm using a cryomicrotome (Leica 3050 S) at −28°C. Sections were placed on glass slides in a drop of deionized water to prevent dehydration. To visualize general anatomical details, sections were subjected to sequential staining in 1% Alcian blue and 0.05% Safranin for 10–30 s each at room temperature, and destaining in deionized water for 10–30 s, as required. Samples were mounted in 60% glycerol for observation. Sections were examined under a Leica M80 stereo microscope with 8-10x magnification or under a Leica MZ 2500 compound microscope with magnification in the range of 100-400x. Photomicrographs were acquired using an attached Leica DFC490 camera. Images were captured either immediately on the same day with freshly stained samples or from samples stored at +4C for a maximum of 1 week.

3 | RESULTS

Phenotypically, witches' broom disease can be seen by the appearance of many new buds, most of which develop into axillary shoots that grow in clumps around the initial infection site to form a broom-like structure, sometimes appearing similar to a bird's nest. (Figure 1a,b). To strengthen the evidence of genetic resistance in birch against witches' broom disease, we examined a collection of 159 infected birch trees (Table S1) identified in the greater Helsinki region (Figure 2a,b). The total number of trees used in the analysis was 721 (234 symptomatic, 487 asymptomatic; Table S1). These data were summarized in a bubble plot (Figure 2c), which suggested that only three sites exhibited clustering; that is, sites that had only symptomatic trees and zero asymptomatic trees (shown in red). In contrast, the overwhelming majority of sites (156 sites) had mixed populations of resistant and susceptible trees. To further investigate this hypothesis, Pearson's chi-squared goodness of fit test with Yates' continuity correction was used, which rejected the null hypothesis that pathogen

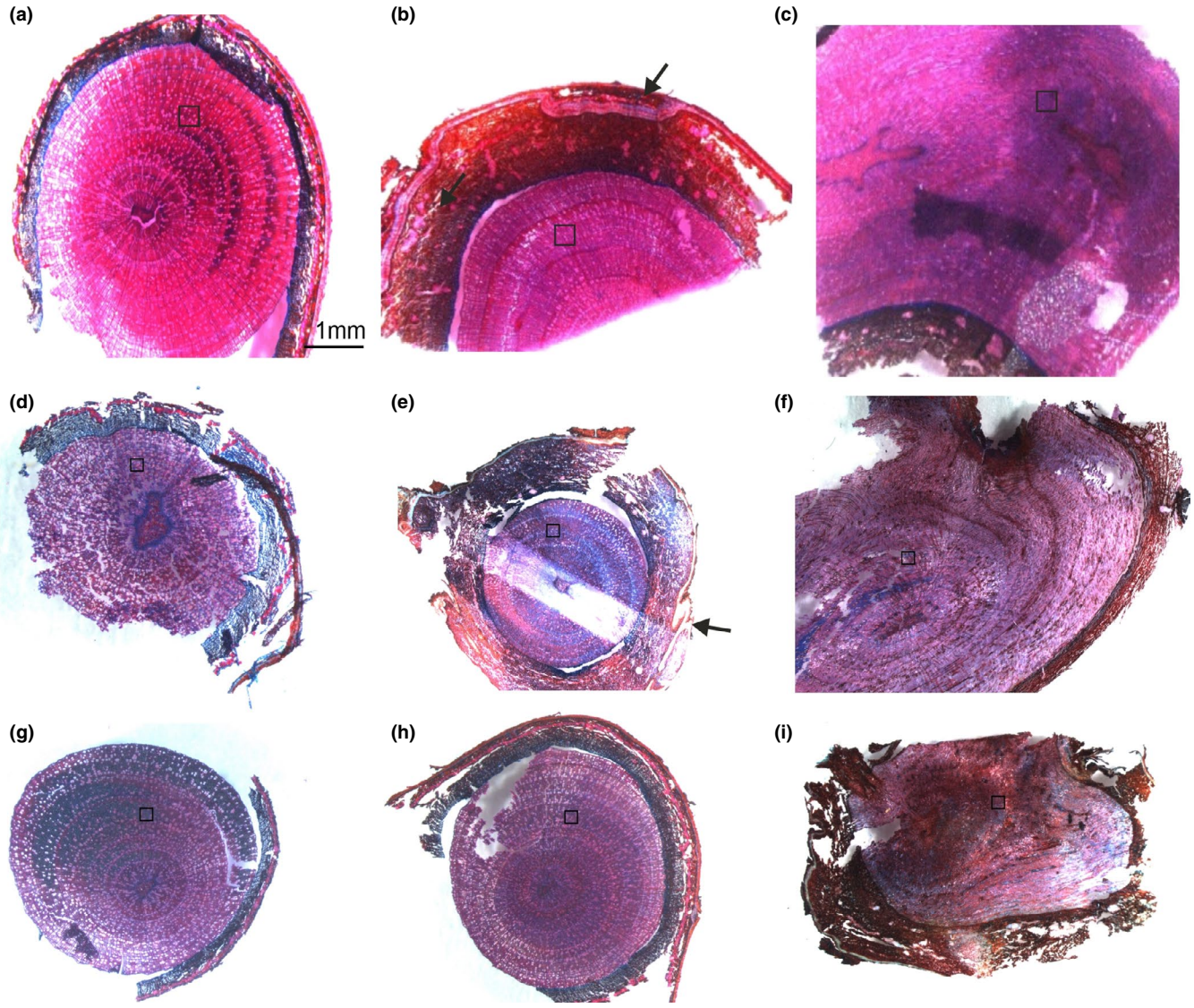

FIGURE 4 Structure of *B. pendula* branches exhibiting broom symptoms. All sections were stained with safranin and alcian blue. Sections from three samples in Figure 3 and listed in Table 2; (a–c) sections from sample one, (d–f) sample two, (g–i) sample three. (a, d, g) Sections from position I in the branch, showing the structure of phenotypically healthy (normal) tissues for comparison (bar = 1 mm; valid for all panels). (b, e, h) Section from position II at the periphery of the infected tissue adjacent to a tumour. Note that in this position, the branch is diseased and swollen in samples one and two, but not three. The black arrow indicates a deformation in the cork cambium. (c, f, i) Sections from position III through the centre of a tumour. The black boxes in all panels indicate the position of the high magnification photographs shown in Figure 5

exposure and environmental conditions determine the distribution of susceptibility (Figure 2). To control for possible biases introduced by planted ornamental trees, we scored all tree groups as either natural plants or planted, totalling 123 and 57, respectively. All sites with only susceptible trees were in natural populations, indicating selection for the planting of ornamental trees did not bias the results.

At the centre of broom, symptoms were tumorous swellings of the woody tissues (Figure 1c–e). Birch tissues at different positions relative to the infection in the same branch were examined microscopically (Figure 4). Compared with normal tissue (Figure 4a,d,g), within the tumour there was enhanced growth of the secondary xylem (Figure 4c,f,i). Generally, xylem tissues were disorganized and tangled in appearance due to the abundant vascular connections feeding the many ectopic buds and shoots (Figure 4c,f,i). Growth within the tumour was also enhanced in both the secondary phloem and periderm.

Comparing swollen (Figure 4b,e) and normal tissues (Figure 4a,d), outside of the vascular cambium, enhanced growth was present in both the secondary phloem and the periderm. Deformations and thickenings were also seen in what appeared to be phellogen or phellem (Figure 4b,e, black arrows). Note that in sample 3, tissues adjacent to the tumour were not swollen (Figure 3c). Comparing tissue adjacent to the tumour (Figure 4h) to normal tissue (Figure 4g), enhanced growth in the secondary phloem and periderm or deformations in the phellogen were not

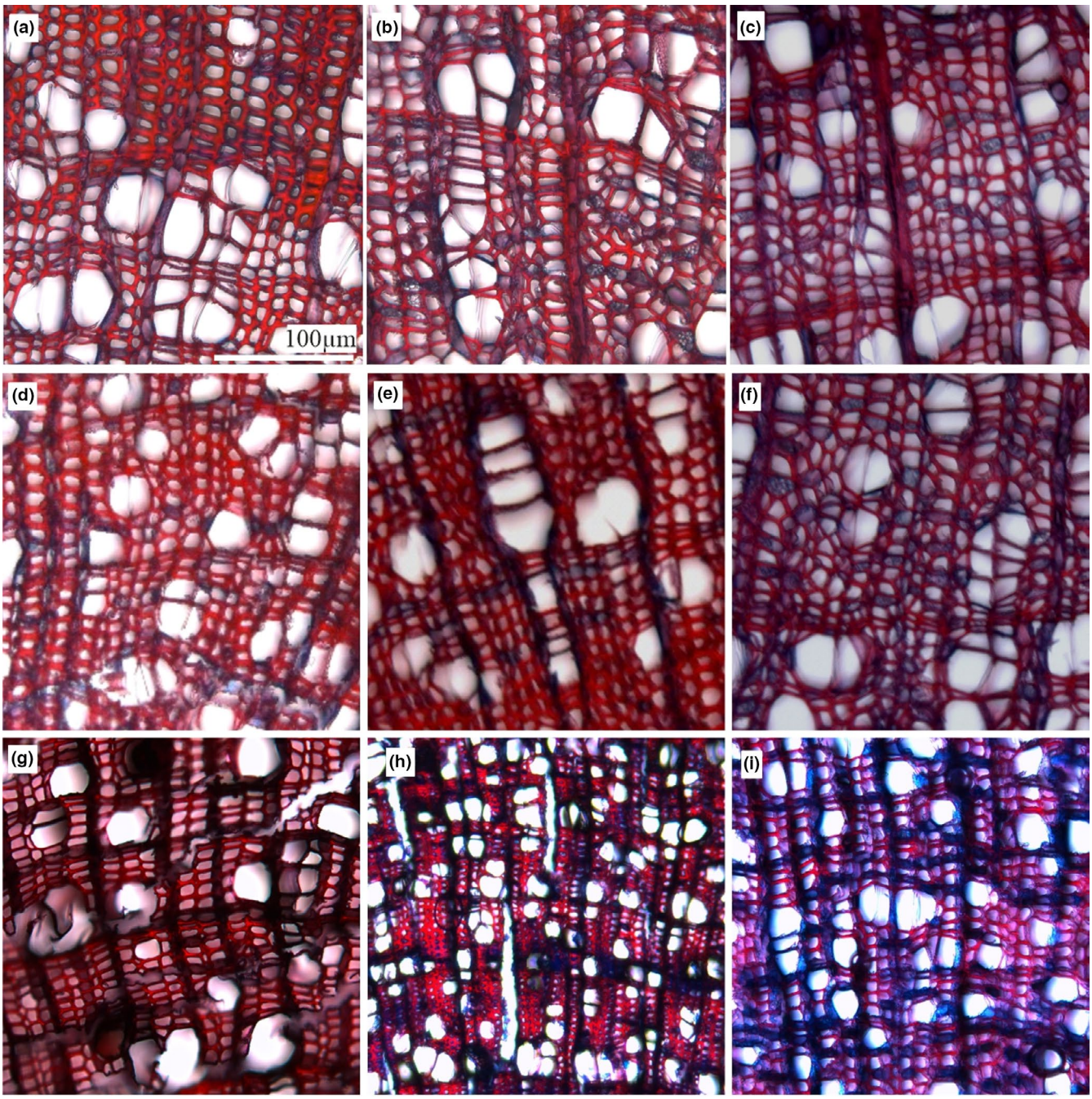

FIGURE 5 Xylem structure of *B. pendula* branches exhibiting broom symptoms. High magnification images showing the details of xylem structure from all sections in Figure 4; (a–c) sections from sample one, (d–f) sample two, (g–i) sample three. (a, d, g) Sections from position I in the branch, showing the structure of phenotypically healthy (normal) tissues for comparison (bar = 100 µm; valid for all panels). (b, e, h) Sections from position II at the periphery of the infected tissue adjacent to a tumour. (c, f, i) Sections from position III through the centre of a tumour. Black boxes shown in Figure 5 indicate the position of these high magnification photographs. Images use magnification in the range of 100–400x

apparent. In the swollen tissues adjacent to the tumour, growth of the xylem was not enhanced (compare Figure 4b,e to Figure 4a,d), suggesting that tumour formation was initiated in the outer tissues of the branch (secondary phloem and the periderm). Samples from tissues adjacent to the tumour did not exhibit clumps of buds and branches (Figure 3) or swollen xylem tissues, suggesting that expansion of the xylem may be associated with the increased vascular connections in the tumour that feed the many branches and buds.

In order to probe the fine structure of xylem tissue, we examined close up micrographs of xylem from normal and infected samples. Blue staining in the xylem was more intense in the sections adjacent to a tumour compared with normal xylem, and still more intense in

sections within a tumour compared with tissues adjacent to the tumour (Figure 5).

4 | DISCUSSION

The anatomy and histology of broom tumours were previously addressed in downy birch (*B. pubescens*; Jump & Woodward, 1994). *Taphrina betulina* infects multiple *Betula* species (Table 1); thus, aspects of tumour morphology in *B. pendula* were addressed, in order to expand on the previous study. Witches' broom symptoms are highly localized with other surrounding tissues remaining normal (Jump & Woodward, 1994). Thus, here an experimental design was used that allows the comparison of normal tissues of the same branch to infected tissue samples. These observations revealed disorganized and swollen xylem, expanded secondary phloem and expanded periderm. Jump and Woodward (1994) made no mention of enhanced growth in the xylem and reported highly expanded secondary phloem, but normal thickness in periderm tissues.

In addition to comparing tumour to normal tissue, as reported by Jump and Woodward (1994), observations were also made in the swollen infected tissues adjacent to tumours. We reasoned that this represents a spreading infection and can give insight into earlier stages of tumour formation. These observations revealed enhanced growth in the secondary phloem and a periderm with enhanced and distorted growth. In both the current study and a previous study (Jump & Woodward, 1994), broom symptoms contained tumorous swellings of the woody tissues where it is assumed that *T. betulina* hyphae have invaded and resided perennially (Mix, 1949). Jump and Woodward (1994) were unable to conclusively determine the location of *T. betulina* hyphae within infected brooms. They did detect fine hyphae-like structures in the middle lamella of secondary phloem cells of broom tumours. However, they were unable to further support this observation using fluorescently labelled wheat germ agglutinin, which binds to chitin in fungal cell walls. Considering that *T. betulina* is known to produce plant growth regulators (Kern & Naef-Roth, 1975) and assuming that the primary tissue colonized by *T. betulina* would be the first to exhibit altered growth, our observation that bark tissues exhibit changes early in tumour expansion in a spreading infection supports the localization of *T. betulina* hyphae in secondary phloem cells reported by Jump and Woodward (1994).

Close up micrographs of xylem revealed differences in staining intensity, which suggests wood chemistry is increasingly altered within the progressively more infected tissues. This observation is consistent with increased lignification previously reported in witches' brooms on downy birch (Jump & Woodward, 1994), although the current study must be interpreted with caution as the staining used is not specific to lignin. Further studies will be required to better understand the nature of altered wood chemistry in broom tumours. Generally, the results reported here are in agreement with the former work on downy birch (Jump & Woodward, 1994), indicating that the basic pathology of *T. betulina* is highly similar on two different host species. Discrepancies between the current work on silver birch and previous study of downy birch may reflect possible differences in tumour formation between birch species.

A prevalence of mixed populations with both resistant and susceptible trees was found at 159 sites in regions around Helsinki, supporting the model that host genotype determines susceptibility to *T. betulina*. Statistical analysis, which rejected the null hypothesis that pathogen exposure or environmental conditions determined susceptibility, further supported that, in these populations of trees (Figure 1), there was segregation of genes that confer resistance to *T. betulina*. This finding strongly suggests that there is genetic resistance against witches' broom disease in birch. However, further genetic studies will be required to confirm this possibility. To this end, controlled crosses between susceptible and resistant individuals are underway with the goal of using fast forward genetics in birch (Alonso-Serra et al., 2020).

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PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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